Atti Soc. ital. Sci. nat. Museo civ. Stor. nat. Milano, 126 (3-4): 201-211, 15-XII-1985

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THE ABSENCE OF EARLY EXPERIENCE ON THE DEVELOPMENT OF AGGRESSIVE BEHAVIOUR IN *LASIUS NIGER* (L.): A CASE OF UNENSLAVED ANT (**)

(*Hymenoptera Formicidae*)

Abstract. — A high level of aggressiveness of *Lasius niger* was first seen when testing its intra- and interspecific (*vs Formica lugubris*) relationships in the laboratory. Subsequently, in order to determine the role of early learning phenomena in the development of aggression in this ant species, 3 groups of artificial colonies were set up containing *L. niger* callow workers hatched on the same day. The control group (cLnA) consisted of ants hatched in the presence of homocolonial adults; the treated experimental group (tLnA) contained workers reared from hatching with *F. lugubris* adults; and the isolated experimental group (iLnA) was set up with newly hatched ants reared together but in isolation from adults. Intra- and interspecific aggressive behaviour of these workers in the 3 categories was quantified 30 days after hatching by pairing them with *L. niger* and *F. lugubris*. The results obtained clearly show that early social experience has no effect on nestmate recognition and the direction of aggression in this ant. In fact, in all the groups there was mutual acceptance by members of the same species; on the contrary overt attacks were always recorded in the heterospecific encounters. This means that isolation from adults does not disturb conspecific recognition. The absence of early learning, as is the present case, could explain why certain ant species have never been found in an enslaved condition.

Riassunto. — *Assenza di esperienze precoci nello sviluppo del comportamento aggressivo in* Lasius niger (*L.*): *il caso di una specie di formiche non schiavizzata* (Hymenoptera Formicidae).

Prove preliminari di laboratorio hanno dimostrato un alto grado di aggressività in *L. niger*, sia a livello intra- che interspecifico (*vs F. lugubris*). In seguito, allo

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(**) This research was supported by grants from M.P.I. and C.N.R. We would like to express our thanks to Dr. P. F. Brain for his critical reading of an earlier draft of the manuscript. Thanks are due to Profs. M. Pavan, G. Ronchetti, and Dr. B. Poldi for their aid in obtaining samples of the two considered species.

scopo di determinare il ruolo esercitato da eventuali fenomeni di apprendimento precoce nello sviluppo del comportamento aggressivo in questa specie di formiche, sono stati allestiti 3 gruppi di colonie artificiali contenenti operaie neonate di *L. niger* schiusesi lo stesso giorno. Il 1° gruppo (cLnA) era formato da formiche nate e cresciute in presenza di operaie adulte omocoloniali; il 2° gruppo (tLnA) conteneva operaie cresciute con adulte di *F. lugubris*; il 3° gruppo (iLnA) era costituito da formiche cresciute assieme, ma in assenza di adulte. Al 30° giorno dalla loro nascita, è stato quantificato, con test a coppie, il comportamento aggressivo intra- ed interspecifico (*vs F. lugubris*) delle operaie dei 3 gruppi. I risultati ottenuti mostrano chiaramente che esperienze sociali precoci non influenzano nè il riconoscimento delle compagne di nido nè la direzione dell'aggressione in questa specie. Infatti, in tutti i gruppi è stata registrata una reciproca accettazione tra i membri della stessa specie; al contrario tutti gli incontri eterospecifici sono stati caratterizzati da attacchi aperti. Ciò significa che anche la crescita in ambiente privo di adulte non altera il riconoscimento dei conspecifici. L'assenza di apprendimento precoce, come in questo caso, potrebbe spiegare perchè certe specie di formiche non sono mai state trovate in natura in condizioni di vera schiavitù.

Introduction.

In ants, the existence of « imprinting-like » processes in the establishment of environmental preferences has been recently demonstrated in *Camponotus vagus* (Scop.) and *Formica polyctena* Först. (Jaisson, 1980). Early olfactory learning has also been described in the ontogeny of cocoon recognition and nursing behaviour by young workers of some species belonging to the *Formica rufa*-group (Jaisson, 1972 c, 1975; Jaisson & Fresneau, 1978; Le Moli & Passetti, 1977, 1978; Le Moli & Mori, 1982). Moreover, in *Formica lugubris* Zett., early experience seems to influence not only brood care but also species recognition and the development of aggressive behaviour (Le Moli & Mori, 1984), as well as an anomalous behaviour (i.e. aggression towards other members of their own colony) is produced by early social deprivation in young workers of *C. vagus* (Morel, 1982, 1983).

It was consequently thought that early olfactory learning could explain the origin and evolution of slavery (or dulosis) in natural dulotic ant societies, since only the species exhibiting this phenomenon could become slaves (Thorpe, 1963; Wilson, 1971; Lorenz, 1973; Le Moli, 1980).

Comparable research on *Lasius niger* (L.) demonstrated that no early experience is needed for recognition of larvae or cocoons and for care behaviour (Lenoir, 1979, 1981; Angeli, 1980). The aim of this study is to determine whether the development of aggression is also unrelated to learning phenomena (i.e. social experience) in this species, possibly explaining why this species has never been found as true slave in nature (Le Moli, 1980).

Materials and methods.

Field sites. Several thousand *Lasius niger* workers (Ln) and worker cocoons were collected from 2 mold colonies, one situated in Mantova (LnA) and one in Pavia (LnB). Moreover, a large number of *Formica lugubris* workers (Fl) and worker cocoons were obtained from a colony situated in a *Larix decidua* wood on around 1200 m on the Monte d'Alpe, in the province of Pavia.

Laboratory conditions. In the laboratory 3 artificial nests were prepared for the heterocolonial individuals of *L. niger* and *F. lugubris,* as carried out in our previous studies (Le Moli & Parmigiani, 1981).

Preliminary test. As *L. niger* was a novel species in this laboratory, a preliminary study on its potential aggressiveness in both intra- and interspecific encounters was carried out. As in previous research on aggressive behaviour in ants (Le Moli & Parmigiani, 1981, 1982), we firstly paired heterocolonial individuals (LnA *vs* LnB) and then contrasted individually *L. niger* with *F. lugubris* (LnA *vs* Fl). No LnA *vs* LnA and LnB *vs* LnB encounters were conducted, since our preliminary observations indicated the complete absence of agonistic patterns in homocolonial context, confirming that in ants aggression is outwardly directed, i.e. extra-colonial (Wallis, 1964).

Experimental test. Nursery boxes were set up with a large number of *L. niger* workers and worker cocoons coming from the colony A. Starting from these conditions, 12 artificial colonies, each containing 50 newly hatched workers, were prepared in 21 × 13 × 6 cm plexiglass boxes. They were divided in 3 batches as follows:

A - Control group (cLnA): colonies 1-4. This batch was set up with young workers removed from the nurseries immediately after eclosion and allowed to mature with 30 homospecific adults (LnA). The floor of these colonies was covered by mold from the original *L. niger* nest.

B - Treated experimental group (tLnA): colonies 5-8. This group contained young workers removed from the nurseries immediately after hatching to minimize the contact with homospecific adults. They were allowed to mature with 30 older workers of *F. lugubris.* Although initially *L. niger* callow workers clustered together, *F. lugubris* workers contacted them almost immediately. There was no fighting between the species, probably because the juveniles release a substance which inhibits attack by adults (Jaisson, 1972 a, b) and this tolerance lasted for the duration of the experiment. The floor of these colonies consisted of a layer of *L. decidua* needles from the original *F. lugubris* ant-hill.

C - Isolated experimental group (iLnA): colonies 9-12. As soon as they hatched, *L. niger* callow workers were taken from the nurseries and then maintained together but in isolation from adults. These colonies were supplied with materials coming both from *L. niger* and *F. lugubris* nests.

All the colonies were maintained at 24 °C and a relative humidity of 65%. The workers were fed on honey diluted in water and *Tenebrio molitor* larvae. Thirty days after hatching, as done in previous researches (cf. LE MOLI & MORI, 1982, 1984), *L. niger* workers belonging to the 3 categories were confronted with *L. niger* adults coming from colony A and with *F. lugubris* ants, both taken from their artificial nest and chosen « outside » the nest, as in previous studies (LE MOLI & MORI, 1984). All the encounters were conducted (as described by LE MOLI & MORI, 1984) in fighting boxes for 15 minutes, and the same indices of behaviour were quantified in seconds: namely mutual investigation (MI), latency to attack (LA), and accumulated attacking time (AAT). The following frequencies were also measured: threat with open mandibles, upright posture, gaster flexing, seizing, dragging, and carrying. The number of animals attacking, the number of attacks delivered, the parts of the body attacked, and the number of injured and or killed ants were also recorded.

Results.

Preliminary test.

Data for this test are presented in Table 1. Encounters between ants belonging to different colonies (LnA *vs* LnB) resulted in an high percentage (80%) of overt combats even if the attacks were not immediate and very extended (see LA and AAT values). During these contests all the elements of conflict behaviour were recorded in the following proportions: threat 85%, gaster flexing 80%, seizing 70%, dragging 45%, carrying and upright posture 30%, startle response 20%. However no encounter was lethal in this time interval. In the other dyads only mutual inspection was performed, although this was accompanied by some aggressive items (mostly threat and upright posture).

All the heterospecific pairs (LnA *vs* Fl) attacked almost immediately without mutual investigation and fought fiercely with prolonged combats. Incidences of aggressive items were: gaster flexing 100%, seizing 95%, carrying 65%, threat 50%, and dragging 35%. Moreover 13 *L. niger* (65%) and 1 *F. lugubris* (5%) were killed during the experimental period.

TABLE 1. — Data from homo- and hetero-specific interactions of *L. niger* workers coming from colony A (LnA) (Medians with ranges).

Paired with	N	Proportion of fighting pairs	MI (s)	LA (s)	AAT (s)	No. of attacks	Killing
L. niger (LnB)	20	16/20 (80%)	109.3 (0-573.4)	188 (1-900)	97.1 (0-853)	2 (0-5)	0/20
F. lugubris	20	20/20	0 (0-5.3)	1 (1-244)	523.5 (5.8-877.2)	1.5 (1-7)	LnA 13/20 (65%) Fl 1/20 (5%)

MI and LA values: *A* differs from *B*, $p < 0.002$.
AAT value: *A* differs from *B*, $p < 0.02$.
No. of attacks value: *A* does not differ from *B*
(Two-tailed Mann-Whitney 'U' test throughout).

Though LA and AAT values suggest a more pronounced and immediate attack *vs F. lugubris*, no significant differences between homo- and heterospecific fighting pairs occurred on these measures (Two-tailed Fisher's exact probability test).

These observations, generally, confirm previous studies on the aggressive nature of other ant species (cf. LE MOLI & PARMIGIANI, 1981, 1982; LE MOLI, MORI & PARMIGIANI, 1982, 1983, 1984). Moreover, the preliminary test shows that *L. niger* is a very aggressive species, since overt attacks occurred not only between heterospecific members (LnA *vs* Fl) but also when heterocolonial individuals were contrasted (LnA *vs* LnB). The high level of intraspecific overt aggression recorded here could be referred to Gause's law in ants (cf. DE VROEY, 1979), but more simply to colony odours in which endogenous (genetic) and exogenous (environmental) factors play a different role.

Experimental test.

A - *Control group.* Data concerning these colonies are presented in Table 2. Members of the same species and colony (cLnA *vs* LnA) never showed agonistic behaviour. At the first contact, the two ants performed only startle responses (30%) and upright postures (45%) which quickly

TABLE 2. — Data from homo- and hetero-specific interactions of *L. niger* workers (cLnA) reared with conspecific adults (LnA) (Medians with ranges).

Paired with	N	Proportion of fighting pairs	MI (s)	LA (s)	AAT (s)	No. of attacks	Killing
A: *L. niger* (LnA)	20	0/20	529.2 (93.3-777.6)	+ 900 (900-900)	0 (0-0)	0 (0-0)	0/40
B: *F. lugubris*	20	20/20	0 (0-0)	1 (1-132.7)	678.6 (9.8-857.2)	1 (1-6)	cLnA 16 (80%) Fl 0/2

MI, LA, AAT, and No. of attacks values: *A* differs from *B*, $p < 0.002$ (Two-tailed Mann-Whitney 'U' Test).

led to very prolonged mutual inspections. Therefore the behaviour of homocolonial individuals was quite different from that showed by heterocolonial members (cf. Table 1).

In contrast, overt attacks occurred in all the heterospecific pairs (cLnA *vs* Fl), as previously seen in the preliminary test. Almost always the ants began to fight immediately after first contact and were still fighting at the end of the experimental period (see LA and AAT values). Gaster flexing and seizing, mainly of the petioles and legs, were always performed, whereas the other items of conflict behaviour which characterized these encounters were as follows: carrying 80%, dragging 65%, and threat 40% of the contexts. Moreover, 80% of *L. niger* workers were killed within 15 minutes.

B - *Treated experimental group.* Data for these colonies are presented in Table 3. Although these ants spent the first period of their life in the presence of heterospecific ants, their encounters with homospecific individuals (tLnA *vs* LnA) generated no sign of aggression. In fact, the ants only investigated each other intensely, without any obvious agonistic pattern. However, the time spent in mutual investigations was not significantly longer (Two-tailed Mann-Whitney 'U' test) than that performed by cLnA *vs* LnA dyads (cf. Table 2). This result clearly suggests that, in these ants, recognition of ones own nestmate and acceptance were immediate and unaffected by early experiences.

TABLE 3. — Data from homo- and hetero-specific interactions of *L. niger* workers (tLnA) reared with heterospecific adults (Fl) (Medians with ranges).

Paired with	N	Proportion of fighting pairs	MI (s)	LA (s)	AAT (s)	No. of attacks	Killing
L. niger (LnA)	20	0/20	335.9 (62-818.9)	+ 900 (900-900)	0 (0-0)	0 (0-0)	0/40
F. lugubris	20	20/20	0 (0-2.8)	1 (1-248.3)	670.5 (187.8-890)	1.5 (1-5)	tLnA 7/20 (35%) Fl 0/20

MI, LA, AAT, and No. of attacks values: *A* differs from *B*, $p < 0.002$ (Two-tailed Mann-Whitney 'U' Test).

When individuals of this batch were paired with *F. lugubris* workers (tLnA *vs* Fl), overt combats were always recorded. The attacks generally followed immediately after contact and were long lasting, as shown by LA and AAT values. When the opponents began the conflict simultaneously (55%), a very violent « scramble » was generated; on the contrary *F. lugubris*, as attacker (40%), generally used the mandibles to seize the opponent's petiole and tried to cut it, whereas *L. niger* clung to the *F. lugubris* antennae or legs and never released them. The contests were so violent that 8 *L. niger* (40%) were killed during the experimental period and a further 7 (35%) after 1 hour. Moreover the aggressive items were performed in the following proportions: gaster flexing and seizing 100%, carrying 90%, dragging 70%, and threat 20%. This shows that also « alien » species was immediately recognized by these *L. niger* workers.

C - *Isolated experimental group.* Data involving these colonies are given in Table 4. As in the other two batches, homospecific encounters (iLnA *vs* LnA) were characterized only by mutual inspection. The time spent in reciprocal interactions by these dyads was statistically similar to that recorded when control and treated *L. niger* workers were paired with homocolonial individuals (Two-tailed Mann-Whitney 'U' test; cf. Tables 2 and 3). The only aggressive pattern performed was upright posture in 50% of the pairs.

TABLE 4. — Data from homo- and hetero-specific interactions of *L. niger* workers (iLnA) maintained in isolation from adults (Medians with ranges).

Paired with	N	Proportion of fighting pairs	MI (s)	LA (s)	AAT (s)	No. of attacks	Killing
A: *L. niger* (LnA)	20	0/20	456.2 (31.8-779.1)	+ 900 (900-900)	0 (0-0)	0 (0-0)	0/40
B: *F. lugubris*	20	20/20	0 (0-0)	1 (1-288)	549 (4-854.9)	1 (1-4)	iLnA 11/ (55%) Fl 2/20 (10%)

MI, LA, AAT, and No. of attacks values: *A* differs from *B*, $p < 0.002$ (Two-tailed Mann-Whitney 'U' Test).

In the heterospecific context (iLnA *vs* Fl), the first meeting led, generally in a short time, to fierce fights during which both ants rolled on the floor in a prolonged combat, as shown by AAT value. However, sometimes, after the contact the antagonists rapidly went away and only at the following meeting showed overt aggression (see LA value). At any rate, the contests were very vigorous and either ant could initiate the conflict (LnA = 20%; Fl = 80%). Gaster flexing was always present, whereas seizing occurred in 95%, carrying in 90%, dragging in 65%, and threat in 30% of the dyads. 55% of the combats were lethal for *L. niger*, while only 2 *F. lugubris* (10%) were killed in the experimental time. Moreover, a further 4 *L. niger* (20%) and 1 *F. lugubris* (5%) were killed after 1 hour.

Conclusions and discussion.

Our results clearly indicate that early experiences in *L. niger* do not affect the nestmate recognition and the development of aggressive behaviour. In fact, both workers reared from hatching with homospecific adults and workers housed from hatching in the presence of *F. lugubris* adults, discriminated between conspecifics and aliens (*F. lugubris*).

Homospecific encounters of the same colony were characterized only by mutual inspection, sometimes accompanied by startle response and

upright posture. In contrast, attacks with virtually no mutual investigation were always recorded in the heterospecific dyads. Moreover, during the combats, all the elements of conflict behaviour were performed, especially seizing and gaster flexing, confirming that *L. niger* is a very aggressive ant species, as besides shown by preliminary test not only at interspecific but also at intercolonial level. Many encounters were lethal, with most individuals of *L. niger* killed, probably because it is smaller than *F. lugubris* and lacks formic acid. Even isolation from adults does not influence the intra- and inter-specific relationships in this ant species. In fact, workers reared without adults from hatching accepted conspecific subjects and fiercely attacked *F. lugubris* ones.

This experimental analysis could lead to a better understanding of the evolution of slave-workers in dulotic ant societies. Data generated by this study, in fact, are in conflict with those previously obtained in similar investigations on *F. lugubris* (LE MOLI & MORI, 1984) where early experience clearly influences the species recognition and could explain its possible existence as slave-worker in nature. This and the other mentioned experimental enquiries on species of the *Formica rufa* group (see Introduction) seem to confirm field observations that several slave species belong to the same *rufa* group. Concerning *Lasius niger* species, LENOIR (1979, and personal communication) demonstrated that young workers not familiar with any kind of larvae (total privation) accept homospecific larvae and nurse them. This fact suggests that this social behaviour requires no early experience during a sensitive period (LENOIR, 1981). Also the absence of early learning phenomena in the interspecific recognition of cocoons (ANGELI, 1980) as well as in the development of aggressive behaviour in *L. niger,* could account for why this species has never been found enslaved in natural ant societies (LE MOLI, 1980). Referring to this point, we can also quote a field observation by CZECHOWSKI (1975) on *Formica sanguinea* predatory expeditions. He observed the robbery of the *L. niger* pupae by *F. sanguinea*; when he later watched the *F. sanguinea* nest, he did not notice any *L. niger* ant in it.

A question that disagrees with our result is why *L. niger* accepts queens of other species, e.g. the temporarily parasitic *L. umbratus*, and takes care of them (BERNARD, 1968). In this case the *niger* workers are able to learn to care for the *umbratus* brood (BUSCHINGER, personal communication, and 1984). Therefore it would be of great interest to study reciprocal relationships (cocoon nursing, aggressive behaviour, olfactory signals) between *L. niger* and the related *L. umbratus* in order to see if a true early experience affects the social behaviour of *L. niger* ant workers.

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